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RESEARCH PAPER

Mapping the global state of invasive alien species: patterns of invasion and policy responses

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Abstract

Aim To use global databases to (1) provide a visualization of global geographical patterns of species invasions, origins and pathways and (2) depict the international uptake of legislative and policy responses to invasive alien species (IAS).

Location Global.

Methods Patterns of recorded species invasions and pathways of introduction were mapped and visualized using data from the Global Invasive Species Database (GISD) and the CABI Invasive Species Compendium (CABI ISC), along with associated legal instruments relevant to IAS compiled from the ECOLEX database. A novel indicator of the asymmetry between each country's 'ingress/egress' of IAS (kappa, K), was developed to further explore spatial patterns.

Results Substantial variation in the spatial patterns of invasion was determined, with the Global North, some newly industrialized countries and small tropical islands being the main recipients of IAS and asymmetry (K) being highest in New World countries and small islands. Of the 1517 recorded IAS, 39% were introduced only intentionally and 26% only unintentionally, 22% both intentionally and unintentionally, while 13% had no information available. The dominant pathway for species invasions was horticulture and the nursery trade, with 31% of the species introduced outside of their natural geographical range. Large increases in legislation on IAS have occurred since the 1990s, particularly for those countries that have high numbers of species invasions.

Main conclusions Clear global patterns in the distributions of IAS are determined, supporting arguments emphasizing the role of colonial history, economic development and trade in driving the human-mediated movement of species. Dominant pathways for species invasions are similar across different regions. Policy responses towards IAS show an increasing desire from the international community to act on species invasions. Current patterns suggest that Africa and Central Asia are priority areas for future IAS research and control.

Keywords

Biogeography, distribution, geographical pattern, global database, international treaties, invasive alien species, legislation, pathways, policy response.

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INTRODUCTION

This paper explores global patterns of invasions, introduction pathways and associated legislative responses for invasive alien species (IAS) based on the most comprehensive databases currently available. IAS are defined in international governance as species introduced via human action outside of their natural geographical range, with a demonstrable environmental or socio-economic impact and capable of sustaining a self-replacing population (IUCN, 2000; Lockwood *et al.*, 2007; Richardson, 2008). Their global impacts are substantial and costly (e.g. Pimentel *et al.*, 2005; Stohlgren & Schnase, 2006; Kettunen *et al.*, 2009; Ricciardi *et al.*, 2011), making species invasions an environmental issue of great global significance.

As a global response to the ongoing threat of IAS, the international community has set the Aichi Biodiversity Target 9 of the Convention on Biological Diversity (CBD, 2010) to ensure that measures to prevent the introduction and establishment of IAS should be in place for all signatories by 2020. Several indicators and mapping efforts have been developed to aid the realization of Target 9, but these are somewhat limited by the geographical focus of reporting countries. McGeoch *et al.* (2010) and Butchart *et al.* (2010) developed global process indicators to monitor Target 9 which report on the number of documented alien species per country and trends in the impacts of IAS on biodiversity, international agreements and national policy responses. The European Environment Agency (EEA, 2012) has also developed indicators, including the cumulative number of invasive species in Europe since 1900, awareness of IAS and a map of the 'worst' species to monitor progress towards Target 9. Understanding patterns of species invasions and the application of international and national legal instruments to control invasions helps identify regions and areas of society where greater effort should be focused. This effort may be facilitated by a visualization of current patterns of invasion.

Maps of the distribution of IAS can be found in databases such as the Early Detection and Distribution Mapping System (EDDMapS, 2016), the CABI Invasive Species Compendium (CABI ISC, 2016) or Delivering Alien Invasive Species Inventories for Europe (DAISIE, 2016). The EEA (2012) uses a map to report on the presence of invasive species and the number of 'worst' IAS per country. van Kleunen *et al.* (2015) mapped the global exchange and accumulation of alien plants and Essl *et al.* (2015) mapped the main pathways of introduction for three types of organisms in Europe. These maps generally focus on a country, region or distribution of a specific type of organism, but there are, to our knowledge, none of the following: global visualizations of the current distribution of IAS in terms of the number of IAS per country, their countries of origin (native range), pathways of introduction and relevant policy responses. This is partly due to bias in species records (Pyšek *et al.*, 2008), difficulties in generating adequate data (because data quality varies) (EEA, 2012) and high uncertainty in the information on species pathways (Hulme, 2015). International databases generated from cross-country cooperative action often act as coordinated systems linking national and regional (more than one country) databases to provide standardized information (Ricciardi *et al.*, 2000). Global databases such as the GISD, CABI ISC or ECOLEX, which record legal instruments globally, have been created to deal with these issues and represent important sources of information that can be effectively utilized to aid pattern visualization and guide the control and management of IAS.

This paper (1) provides a visualization of global geographical patterns of species invasions, their origin and pathways of introduction using global databases and (2) depicts the international uptake of legislative and policy responses to IAS.

METHODS

In this section we discuss the methods used to: (1) compile and clean IAS data and legal instruments associated with IAS, including international treaties, national/subnational legislations and regulations, and (2) analyse the data. We used data from three major global databases: GISD, ECOLEX and CABI ISC. GISD (2016) and ECOLEX (2016) were commissioned by the International Union for Conservation of Nature (IUCN); CABI ISC (2016) was developed by a consortium of governmental/non-governmental organizations. IAS records were provided by GISD (2016) and CABI ISC (2016) and legal instruments compiled from ECOLEX (2016). These databases (GISD, CABI ISC and ECOLEX) are discussed in more detail below. A list of the abbreviations and variables used in this paper is given in Table 1.

Invasive alien species: GISD and CABI ISC

We performed a survey of major databases focusing on alien species and IAS, including CABI ISC (2016), GISD (2016), the North European and Baltic Network of Invasive Species (NOBANIS, 2016) and DAISIE (2016). The two most comprehensive databases, GISD and CABI ISC, provide information on alien species globally, including their invasive range, native range and introduction pathways. Both databases were created in response to the need for a global information system on invasive species and to enable the distributions of IAS to be mapped (Ricciardi *et al.*, 2000; CABI ISC, 2016). The species records used include local and country distribution, status and organism type. Table S1 in the Supporting Information gives the terms used in the GISD and CABI ISC databases with respect to species occurrence and invasiveness. Information within the GISD and CABI ISC databases is compiled from an array of sources including scientific papers and regional species databases and is reviewed by international expert contributors (GISD, 2016; CABI ISC, 2016). Although both databases are limited to some extent by geographical and taxonomic bias and incompleteness (Westphal *et al.*, 2008; McGeoch *et al.*, 2010), they are the databases best suited to our study as they provide freely accessible comprehensive data across all recorded taxonomic groups globally.

Table 1 List and description of (a) abbreviations and (b) variables.

(a) Abbreviations

Abbreviation	Description
ACC	Acclimation societies, botanical gardens, zoos
AG	Agriculture
AQ	Aquaculture, fisheries, aquarium release
BC	Biological control
CABI ISC	CABI Invasive Species Compendium
CBD	Convention on Biological Diversity
DAISIE	Delivering Alien Invasive Species Inventories for Europe
EC	Erosion control, ecological restoration, land reclamation
FAO	Food and Agriculture Organization (of the United Nations)
FOR	Forestry, agroforestry
GEF	Global Environment Facility
GISD	Global Invasive Species Database
HDI	Human Development Index
HORT	Horticulture, nursery trade, ornamental purposes
IAS	Invasive alien species
INR	Invasive native range
IP	Ignorant possessions, stowaway, assisted transport through trade via road vehicles, trains, boats, planes
IR	Intentional release, landscape improvement, angling, sport, smuggling
ISO	International Organization for Standardization
IUCN	International Union for the Conservation of Nature
MIL	Military equipment, military movement, landmine detection, war experiments
NA	No information available
ND	Natural dispersal, floating vegetation debris
NOBANIS	North European and Baltic Network of Invasive Species
SHIP	Ballast water, ship biofouling
TRA	Food trade, pet and aquarium trade, fur trade, internet sales, research, transportation of machinery and domesticated animals
UN	United Nations
UNDP	United Nations Development Programme
UNEP	United Nations Environment Programme
USDA	United States Department of Agriculture
VT	Vector transmission/transportation

(b) Variables

Variable	Definition	Data source
K	Species asymmetry index. Measures the level of asymmetry within a country between the number of invasive species within the country and the number of native species invasive elsewhere	See equation 1
A	Total land area of a country (km^2), excluding the area under inland water bodies, national claims to continental shelf, and exclusive economic zones	World Bank (2014)
N_{IT}	Number of international treaties subscribed to by each country	ECOLEX (2016)
Population	All residents irrespective of legal status or citizenship	World Bank (2014)
S_{Inv}	Number of IAS in a given country	GISD (2016), CABI ISC (2016)
S_{InvT}	Total number of recorded IAS in the databases; S_{InvT}= 1517 species	GISD (2016), CABI ISC (2016)
S'_{Inv}	S_{Inv} divided by S_{InvT}	GISD (2016), CABI ISC (2016)
S_{Nat}	Number of species native to a country but invasive elsewhere	GISD (2016), CABI ISC (2016)
S_{NatT}	Total number of recorded IAS in the databases that have native range information; S_{NatT}= 1140 species	GISD (2016), CABI ISC (2016)
S'_{Nat}	S_{Nat} divided by S_{NatT}	GISD (2016), CABI ISC (2016)

In the present methodology, IAS are considered to be species classified as both 'alien' and 'invasive' in the GISD and 'introduced' and 'invasive' in the CABI ISC (Table S1). Species with 'occurrence' (or 'distribution' in the CABI ISC) listed as 'recorded in error', 'absent' or 'eradicated' were excluded. This was to avoid duplication of data and focus the research on IAS as defined in the Introduction.

The invasive native range (INR) for each IAS was also determined, when available; this refers to the native range (countries of origin) of each IAS based on information in the GISD and CABI ISC. The INR includes countries in which the IAS is categorized as 'native endemic', 'native' and 'native non-endemic' (Table S1). IAS records for which information on the INR was not available were excluded from the INR analysis. Data from both databases were carefully checked for errors, inconsistencies or duplications, refined as appropriate and then used to map the global geographical distribution of recorded IAS, showing both countries of origin (based on the INR) and countries 'invaded'. For each country, the number of IAS established in that country and the number of IAS native to that country but invasive elsewhere were calculated.

Environmental IAS treaties, legislation and regulation: the ECOLEX database

Databases with records of international treaties and environmental national/sub-national legislation and regulations pertaining to IAS were scrutinized. These types of records can be hard to locate and difficult to access as they tend to be scattered across governmental/non-governmental databases and websites. Definitions we use here include (Cane & Conaghan, 2008): *legislation* (Cane & Conaghan, 2008, p. 726) 'written rules of law ... authoritatively ratified' and *regulations* (Cane & Conaghan, 2008, p. 996) 'legal rules, which ... steer behaviour of mainly private citizens and companies but also ... central/local government [and] public agencies'. We use the term *legal instruments* in reference to international treaties, regulations and legislations.

Some legal instruments referring to invasive species can be found on specific databases or IAS specialist websites such as the USDA National Invasive Species Information Center (2016), the GB Non-Native Species Secretariat (2016) and Invasive Species South Africa (2016). The ECOLEX (2016) database was developed by the IUCN, the Food and Agriculture Organization of the United Nations (FAO) and the United Nations Environment Programme (UNEP) to consolidate information on global environmental law, ranging from international treaties to national legislation and technical guidance documents. This database was thus considered to be the most comprehensive available, having both ease of access and good search functionality (e.g. the ability to search documents using keywords).

Two searches were conducted within ECOLEX (2016) to extract (1) international treaties and (2) national legislation and regulations relevant to IAS. This paper's scope is global and therefore includes signatory and non-signatory countries of the Convention on Biological Diversity (CBD, 2010). A keyword search within ECOLEX was used to determine the number of international treaties mentioning invasive species. Keywords used (including plural variants) were: 'alien', 'invasive', 'exotic', 'non-indigenous', 'non-native', 'pest' and 'introduced species'. For each international treaty returned, the name, nature, legal instrument date, keyword used and article were recorded and the list of participating countries extracted. Overseas territories were assigned the same number of international treaties they are signatory to as their sovereign state, e.g. Guadeloupe was assigned the same number of treaties as France.

The ECOLEX database includes 'alien species' in document keywords, which facilitates the search process. However, for consistency, the same keywords used in the international treaty search (within ECOLEX) were used to compile national legislation and regulation records that mention/are relevant to invasive species. The ECOLEX database was searched using English keywords only. All instruments returned from the search were assigned an integer 'relevance score' from 0 to 4 to differentiate legal instruments based on their degree of focus on IAS:

0, not relevant for alien species;

1, mentions alien species but has no proposed actions;

2, mentions alien species with expression of action or potential for action;

3, assigned to a document where a section, paragraph or chapter is dedicated to IAS prevention, control or management;

4, >50% of the document is dedicated to alien species.

Further details on these criteria are given in Table S2.

Documents that used the terms 'alien', 'non-native', or 'non-indigenous' in a non-IAS context were eliminated, as were those referring to 'invasive procedures'. Documents in languages other than English (39% of the documents returned), but found using English keywords, were translated with the help of Google Translate. For each legal instrument, the country or countries, territorial subdivision, ECOLEX ID, title of text, date of text and relevance score were recorded (see Table S4). Only international treaties, relevant national/sub-national regulations and legislations (relevance score > 0) were considered for the data analysis; miscellaneous documents were rejected.

Data analysis

From the results of our searches described above, we (1) calculate an asymmetry index for IAS ingress/egress to a given country, and (2) map (visualize) the results of these and other IAS metrics.

First, an IAS asymmetry index K (kappa) was developed to highlight the imbalance of ingress/egress of IAS for a given country:

$$K=6\frac{S'_{Inv}-S'_{Nat}}{S'_{Inv}+S'_{Nat}} \quad (1)$$

where S'_{Inv} is the number of IAS in a given country (S_{Inv}) divided by the total number of recorded IAS in the GISD and CABI ISC databases ($S_{InvT} = 1517$). S'_{Nat} is the number of species native in a given country but invasive elsewhere (S_{Nat}) divided by the total number of recorded IAS in the databases for which INR information was available ($S_{NatT} = 1140$; 377 species lacked native range data). The S_{Inv} and S_{Nat} used to calculate K exclude overseas territories. An arbitrary factor of 6 was used, resulting in a scale ranging from −6 to 6, indicating the imbalance between ingress/egress of IAS of a given country. A positive (negative) K value indicates a country that has more (fewer) IAS than species native to that country that are invasive elsewhere. For instance, $S_{Inv} = 7$ (S'_{Inv}=0.005) and $S_{Nat} = 121$ (S'_{Nat}=0.106) gives K = −5.5 and $S_{Inv} = 322$ and $S_{Nat} = 117$ gives K = 2.1.

Second, for visualization, global maps were produced to show S_{Inv}, S_{Nat}, K and the number of international treaties (N_{IT}). Chord diagrams show pathways to/from a geographical region for all IAS and by type of organism. Country data are matched using ISO3 codes (ISO, 2016). The geographical regions used are the seven UNEP (2012) GEO regions: Africa, Asia plus Pacific, Europe, Latin America plus the Caribbean, North America, West Asia and the Polar Regions.

RESULTS

Here we report on patterns of (1) invasions and IAS native range, (2) pathways and (3) policy response.

Patterns of invasion

The IAS records extracted from the combined GISD (2016) and CABI ISC (2016) databases, utilizing the criteria given above, spanned 243 countries and overseas territories, with 1517 different species represented. As shown in Fig. S1, results included 886 terrestrial plants, 222 arthropods, 72 mammals, 66 fish, 52 aquatic plants, 37 birds, 21 reptiles, 14 amphibians and 147 other organisms. Figure 1(a) shows the number of IAS per country (S_{Inv}) based on the GISD (2016) and CABI ISC (2016) databases. Results (excluding overseas territories) ranged from $1 \le S_{Inv} \le 523$ IAS per country (median 24, mean 44 IAS per country). Results (including overseas territories) were $1 \le S_{Inv} \le 1071$ IAS per country (median 24, mean 55 IAS per country). Over 85 countries (excluding overseas territories) have $S_{Inv} \le 15$, with 42% of these countries being located in Africa and West Asia; 19 countries have $S_{Inv} \ge 100$. The 10 countries with the highest number of recorded IAS (excluding and including overseas territories) are listed in Table 2. The country with the greatest number of recorded IAS excluding overseas territories is the USA (including Hawaii) ($S_{Inv} = 523$) followed by New Zealand ($S_{Inv} = 329$); including overseas territories it is the USA ($S_{Inv} = 1071$) followed by France ($S_{Inv} = 927$).

In Fig. 1(b), the number of IAS per country (S_{Inv}) was normalized by the country's land area A (km^2) (excluding inland water bodies). Figure 1(a, b) shows that the economically developed Global North along with some newly industrialized countries (e.g. South Africa, China, India, Brazil) have generally received the most IAS, but also that small tropical and sub-tropical islands in particular have high numbers of IAS per km^2. The circles in Fig. 1(a, b) illustrate the number of IAS in countries with a land area $A < 20{,}000$ km^2. As emphasized in Fig. 1(b), 61 (80%) of the 76 small islands with recorded IAS and $A < 20{,}000$ km^2, had >0.01 species per km^2.

Based on the GISD (2016) and CABI ISC (2016) search results, for 97% [88%] of countries (excluding overseas territories), the dominant [second most dominant] IAS organism group in a given country was terrestrial plants [arthropods]. Overall, IAS type (number of countries where recorded) was: terrestrial plants (236 countries), arthropods (217), aquatic plants (110), mammals (147), fish (146), birds (82), reptiles (53) and amphibians (53). The IAS with the greatest recorded international presence, per organism group, are listed in Table 3.

Many countries have a number of species native to that country that have become invasive elsewhere; we represent these using the variable S_{Nat} and plot them globally in Fig. 2. Just under 55% of the 243 countries (excluding overseas territories) have 'exported' 56 or more recorded species (i.e. $S_{Nat} \ge 56$); 16% have $S_{Nat} \ge 126$. The five countries that contribute the most IAS to other countries are China (S_{Nat} =257), India ($S_{Nat} = 230$), Mexico ($S_{Nat} = 218$), Turkey ($S_{Nat} = 193$) and France ($S_{Nat} = 186$) with the Asia Pacific region being the biggest 'exporter' of IAS, with 603 species native to that region being invasive elsewhere. Nearly 55% (32 out of 58) of countries in the Africa region have a low number of recorded species that have become invasive elsewhere ($S_{Nat} < 56$).

In Fig. 3 we present the results for our IAS asymmetry index (K, equation 1). Sixty-one (25%) of the 243 countries (excluding overseas territories) have K > 0.0, meaning that more species are invasive in those countries than there are native species from those countries that are invasive elsewhere, while 182 (75%) countries have K < 0.0. Forty-seven (89%) of the 53 countries with K > 0.0 are islands (K > 4.0 for 17 of these 47 islands), while the five territories with the highest K are New Zealand (K = 4.9), the USA (K = 3.1), Australia (K = 2.1), Canada (K = 1.8) and South Africa (K = 1.3. The five territories with the lowest K ($-5.6 \le K \le -5.4$) are Mongolia, Afghanistan, the Democratic People's Republic of Korea, Azerbaijan and Kyrgyzstan. The number of recorded IAS (S_{Inv}), the number of native invasive species per country (S_{Nat}) and K for each country are given in Table S3.

Pathways

Pathways of introduction describe how a species is transported, intentionally or unintentionally, outside its natural

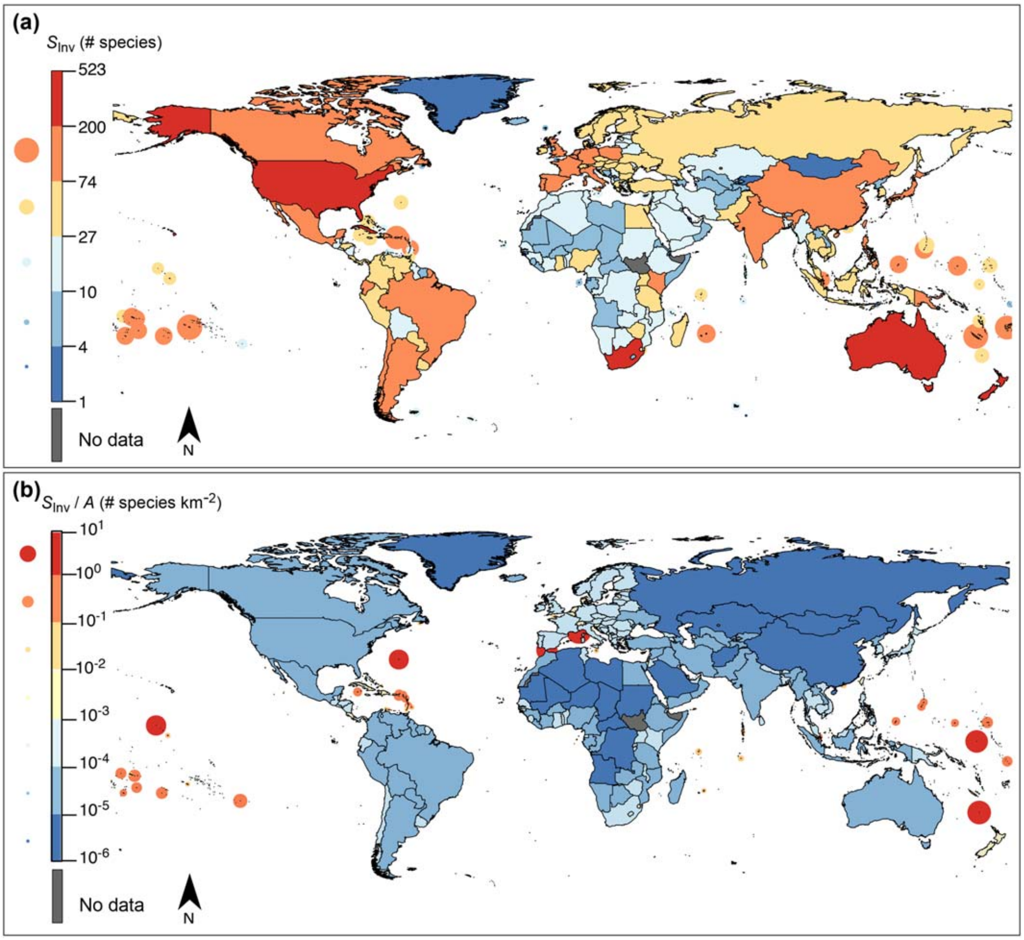

Figure 1 Global map of the number of invasive alien species (IAS) per country, excluding overseas territories, based on the Global Invasive Species Database (GISD, 2016) and the CABI Invasive Species Compendium (CABI ISC, 2016). The total number of IAS recorded in the two databases is $S_{InvT} = 1517$. Shown are (a) S_{Inv} (the number of recorded IAS per country) and (b) normalized IAS values, S_{Inv}/A, where A is the land area of the country in km^2 excluding inland water bodies. For both (a) and (b), the scale increases logarithmically. To aid visualization of smaller land areas, circles represent countries with $A < 20,000$ km^2. The circle diameter and colour are both linked to the number of IAS (S_{Inv}) such that red circles are larger than blue circles. The circles are located based on the centroid of the country. Maps were generated in R (v.3.2.2) using the rworldmap package. Map projection lines and projections are from the Natural Earth (2016) data (v.1.4.0) at a scale of 1:110 and use the geographical coordinate system (projection) WGS84.

Table 2 The 10 countries with the highest S_{Inv} (number of recorded invasive alien species, IAS), including and excluding overseas territories. Also shown is S_{Inv} divided by country land area A (km^2) (excluding inland water bodies) and multiplied by 10^5, resulting in the equivalent number of IAS per 100,000 km^2. Based on data from GISD (2016) and CABI ISC (2016). See Table S3 for detailed information (excluding overseas territories) for all countries.

Country (excluding overseas territories)	S_{Inv} (species)	(S_{Inv}/A) ($\times 10^5$) (species per 100,000 km^2)	Country (including overseas territories)	S_{Inv} (species)
1. USA	523	5.7	1. USA	1071
2. New Zealand	329	124.9	2. France	927
3. Australia	322	4.2	3. New Zealand	511
4. Cuba	318	298.8	4. Australia	465
5. South Africa	208	17.1	5. UK	463
6. French Polynesia	190	5191.3	6. Cuba	318
7. New Caledonia	183	1001.1	7. China	220
8. Reunion	173	6889.7	8. South Africa	208
9. Fiji	167	914.1	9. Fiji	167
10. Canada	166	1.8	10. Canada	166

Table 3 Top five invasive alien species (IAS) with the greatest international presence for each of the following organism groups: terrestrial plants, arthropods, mammals, fish and aquatic plants. The occurrence is number of countries (excluding overseas territories) with a given IAS, out of 243 countries overall in our database with IAS. Introduction pathways (defined in Table 1(a) and obtained from GISD, 2016 and CABI ISC, 2016) are given for each species. Species in bold type feature in the list of the top 100 worst invaders (Lowe *et al.*, 2000).

Species	Common name	Occurrence: no. of countries [% of 243 countries]	Main introduction pathways
Terrestrial plants			
Cyperus rotundus	Purple nutsedge	91 [37%]	AG, HORT, SHIP
Lantana camara	**Blacksage**	**87 [36%]**	**HORT**
Ricinus communis	Castor-oil plant	76 [31%]	HORT
Leucaena leucocephala	**Leucaena**	**66 [27%]**	**ACC, AG, HORT, TRA**
Cynodon dactylon	Bermuda grass	49 [20%]	IP
Arthropods			
Icerya purchasi	Cottony cushion scale	103 [42%]	AG, TRA, VT
Tapinoma melanocephalum	Ghost ant	98 [40%]	IP
Aphis spiraecola	Spirea aphid	89 [37%]	HORT, IP, VT
Cryptotermes brevis	Powderpost termite	57 [23%]	TRA
Frankliniella occidentalis	Western flower thrip	54 [22%]	AG, HORT, IP
Mammals			
Rattus rattus	**Black rat**	**56 [23%]**	**IP**
Felis catus	**Domestic cat**	**54 [22%]**	**IR, TRA**
Mus musculus	**House mouse**	**36 [15%]**	**IP, TRA, MIL,**
Myocastor coypus	**River rat**	**32 [13%]**	**TRA,**
Rattus exulans	Pacific rat	32 [13%]	IR
Fish			
Gambusia holbrooki	Eastern mosquitofish	72 [30%]	AQ, HORT, IR, TRA, ACC, SHIP
Hypophthalmichthys molitrix	Silver carp	62 [26%]	
Hypophthalmichthys nobilis	Bighead carp	55 [23%]	
Poecilia reticulata	Rainbow fish	41 [17%]	
Cyprinus carpio	**Common carp**	**21 [9%]**	
Aquatic plants			
Eichhornia crassipes	**Water hyacinth**	**73 [30%]**	**HORT, TRA, IR, IP**
Salvinia molesta	Water fern	32 [13%]	ND, HORT, TRA, IP
Elodea canadensis	Common waterweed	22 [9%]	HORT, TRA, IP
Egeria densa	Leafy elodea	18 [7%]	TRA
Sargassum muticum	Wire weed	17 [7%]	AQ, ND

geographical range. Using chord diagrams to visualize relationships between IAS, introduction pathway and geographical regions, Fig. 4 depicts the possible number of IAS that ingress (egress) to (from) a geographical region intentionally (Fig. 4a (4c)) or unintentionally (Fig. 4b (4d)) for each identified introduction pathway. The upper half of the circle of each chord diagram includes the seven UNEP (2012) geographical regions; the bottom half includes a subset of the 14 introduction pathways (see Table 1(a) for abbreviations). The values on the circumference of each chord diagram represent the cumulative number of IAS per region or per pathway and 'include' duplicates, because species can be introduced to multiple regions via different pathways. The thickness of chords where they touch the edge of each circle represents the number of species for a given pathway/geographical region, as determined by the scale on the circumference of each circle. For instance, Fig. 4(a) shows that the introduction pathway 'Horticulture' (HORT) has intentionally introduced 116 species in Europe. The patterns in Fig. 4(a/c) are highly similar; the main differences are in terms of number of species. For instance, West Asia 'exports' a higher number than it 'imports' as opposed to Europe, which 'imports' more than it 'exports'. Of the 1517 species recorded as IAS in our databases, 594 (39%) are likely to have been introduced just intentionally, 401 (26%) just unintentionally, 332 (22%) both intentionally and unintentionally; 191 species (13%) had no pathway data available.

HORT is the largest pathway for intentional (Fig. 4a) introduction of IAS. Further data analysis indicates that between the seven global regions, after removing duplicate species, HORT has 465 unique IAS (31% of the 1517 species in our databases) introduced globally. This is largely due to the bias in plant records in both the GISD (2016) and the

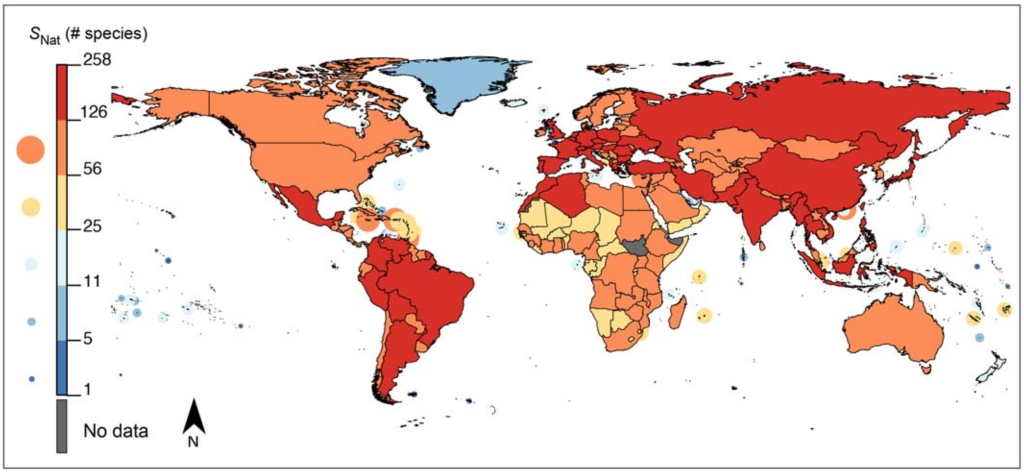

Figure 2 Global map of S_{Nat}, the number of species native to a country but considered invasive alien species (IAS) in other countries, as based on the Global Invasive Species Database (GISD, 2016) and the CABI Invasive Species Compendium (CABI ISC, 2016). The total number of IAS with native range information recorded in the two databases (S_{NatT}) is 1140. As an example, *Rattus rattus* is classified as an IAS in 59 countries but is recorded as native in China. China is the native country of 257 species recorded as IAS in other countries (S_{Nat}). All other information on the legend, circles and mapping source is the same as for Fig. 1.

CABI ISC (2016); indeed 95% of the 465 IAS introduced via the HORT pathway are terrestrial and aquatic plants (the remaining 5% being amphibians, birds, fish, mammals and other organisms introduced for ornamental purposes).

'Trade' (TRA) (pet/aquarium trade, live food trade, online sales, industry, etc.) and 'Intentional release' (IR) (sports, fishing, hunting, medicinal purposes, research or via smuggling) are the second and third largest pathways for intentional (Fig. 4a) introduction of IAS with (after removing duplicates between geographical regions) 226 (15%) and 214 (14%), respectively, of 1517 species introduced globally.

As shown in Fig. 4(a) (intentional ingress) and 4c (intentional egress), geographical regions follow similar trends,

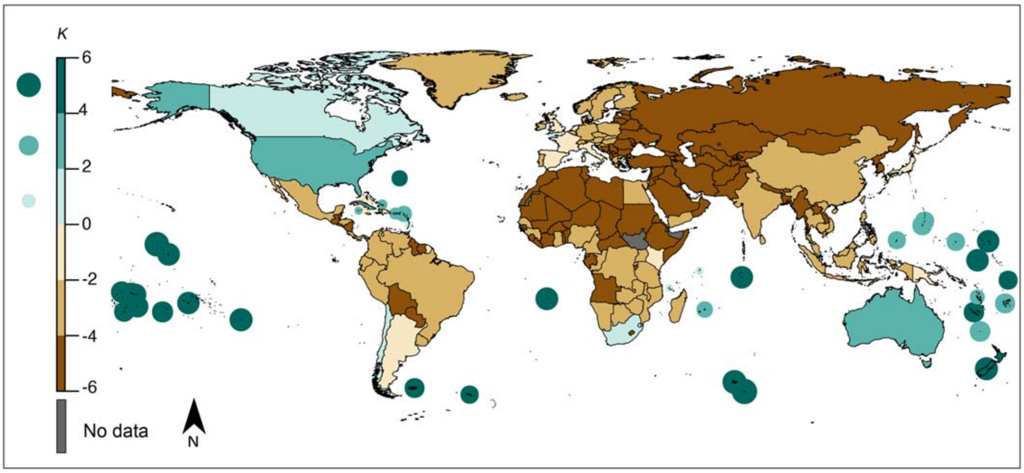

Figure 3 Global map of invasive alien species (IAS) asymmetry index, K, indicating the asymmetry between each country's 'ingress/egress' of IAS. The IAS asymmetry index K for a given country is given by equation 1, $K=6[(S'_{Inv}-S'_{Nat})/(S'_{Inv}+S'_{Nat})]$, where S'_{Inv} is the number of IAS per country (S_{Inv}) divided by the total number of recorded IAS in the GISD (2016) and CABI ISC (2016) databases ($S_{InvT}=1517$) and S'_{Nat} is the number of species native in a country but invasive elsewhere (S_{Nat}) divided by the total number of recorded IAS in the databases for which information about invasive native range was available ($S_{NatT}=1140$; 377 species lacked native range data). A positive [negative] K value indicates a country that has more [fewer] IAS than species native to that country that are invasive elsewhere. For instance, for South Africa $K=1.3$ and there are more IAS recorded in South Africa than species native to South Africa that are invasive in other countries. All other information on circles and mapping sources is the same as for Fig. 1.

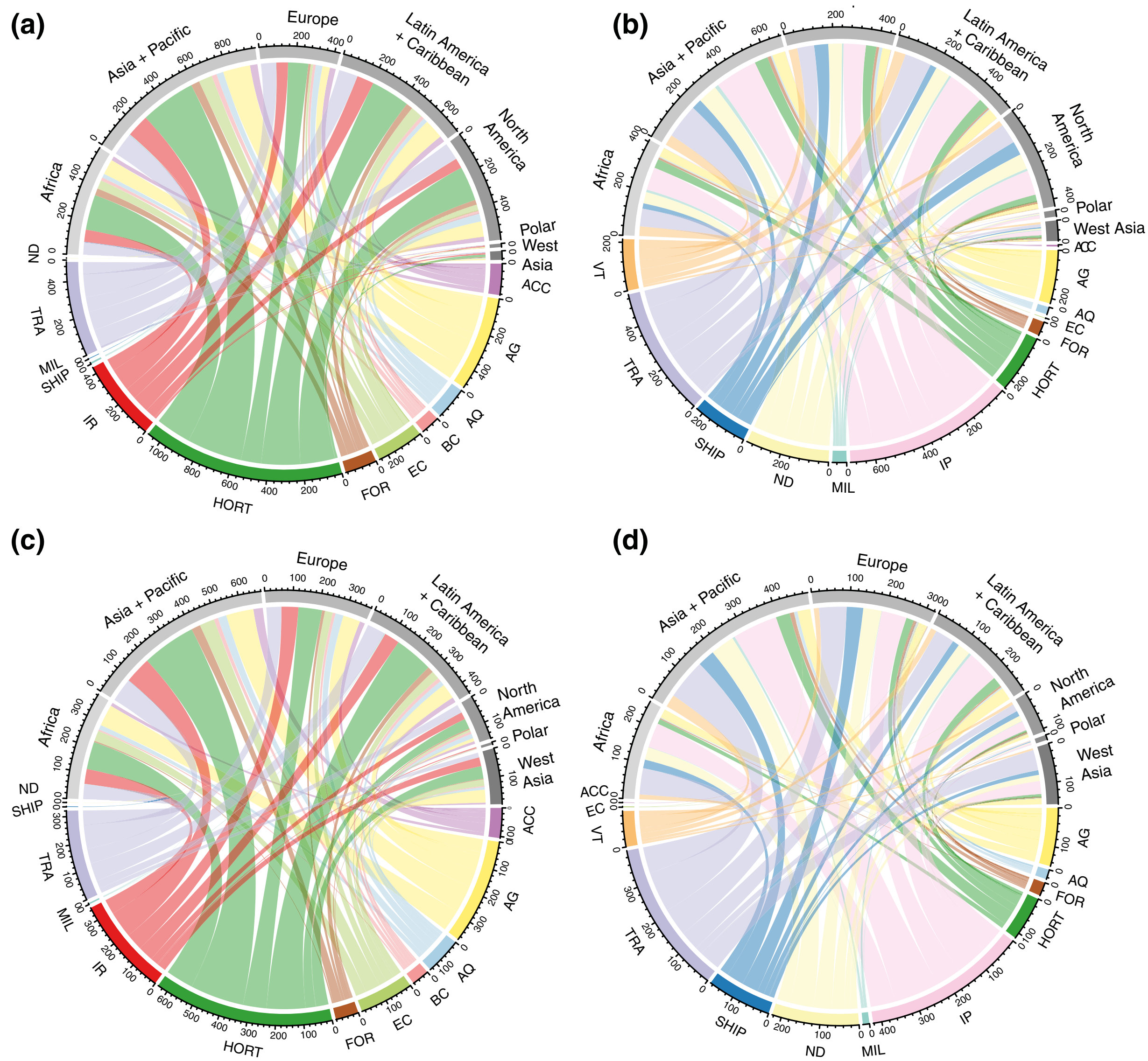

Figure 4 The number of invasive alien species by introduction pathways to [from] a geographical region using chord diagrams (see text): (a) intentional ingress, (b) unintentional ingress, (c) intentional egress and (d) unintentional egress. Data are from CABI ISC (2016) and GISD (2016). Abbreviations for introduction pathways are given in Table 1(a). See the text for a detailed description of the chord diagram. See Figs S2–S5 for chord diagrams broken down by organism type and the number of IAS that ingress and egress to a geographical region intentionally and unintentionally.

with HORT being the main pathway for ingress and egress of IAS to all regions except for the Polar region, followed by 'Agriculture' (AG).

Figures S2–S5 show chord diagrams, broken down by organism type, for the number of IAS that ingress/egress to a geographical region intentionally/unintentionally. Figure S2 shows that 407 (46%) and 188 (21%) of 886 unique terrestrial plants (Fig. S2a) are introduced intentionally through HORT and AG, respectively, 31 (47%) and 29 (44%) of 66 unique species of fish (Fig. S2c) are introduced through 'Aquaculture' (AQ) and TRA, respectively, and 28 (39%) and 23 (32%) of 72 unique species of mammals (Fig. S2d) are introduced via IR and TRA, respectively. Further data analysis shows that the percentage of the total invasive terrestrial plants recorded as introduced for each region through HORT is >50% for Africa, Asia Pacific, Europe, North America and West Asia and 39% in Latin America and the Caribbean. Intentional introductions of fish through AQ vary from 47% of recorded invasive fish in North America to 81% in Africa. Just over 50% of mammals introduced intentionally to Europe were 'imported' through TRA. Intentional introductions of reptiles through TRA vary from 50% of recorded invasive reptiles in Europe to 90% in North America.

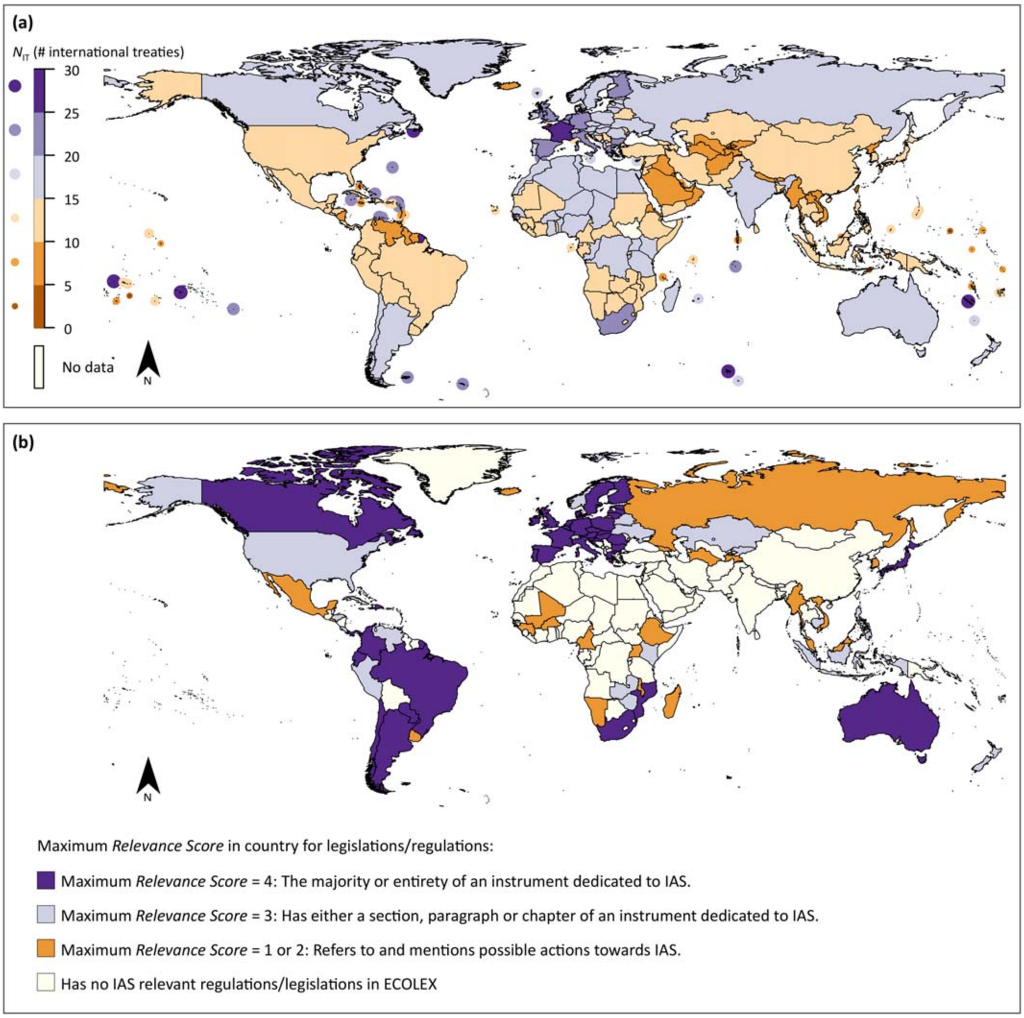

Figure 5 Global map of legal instruments (1933 – 2015) relevant to invasive alien species (IAS) based on data from ECOLEX (2016). Shown are (a) N_{IT} (number of international treaties mentioning IAS that each country is signatory to, including global and regional treaties for 1933 – 2015) and (b) map of the maximum relevance score for each country that has national/sub-national regulations/legislation in place, relevant to IAS (1980 – 2015). Overseas territories have been allocated the same number of international treaties as their sovereign state. This map depicts a global view of where national/sub-national legislation/regulations (relevance score > 0) are in place and the differences in database input across countries; the USA for instance has one legal document, which has a Relevance Score of 3, recorded in ECOLEX despite having more legal instruments in part or entirely dedicated to IAS that are not in ECOLEX (2016). All other information on circles and mapping source is the same as that for Fig. 1.

As shown in Fig. 4(b) (unintentional ingress) and 4(d) (unintentional egress), 'Ignorant possessions' (IP) and 'Assisted transportation' (TRA) (transportation of machinery, equipment, soil, etc.) are the main pathways for unintentional introduction of IAS across regions, followed by 'Natural dispersal' (ND) (natural disasters, floating debris, use of human-modified waterways, etc.), HORT and 'Shipping ballast water/hull fouling' (SHIP). Further analysis of the data shows that unintentional introductions in each region range from 44% of recorded IAS in Latin America and the Caribbean, to 75% of recorded IAS in West Asia. Arthropods and marine organisms are the dominant organisms for unintentional introduction across all organism types with 91% of arthropods and 88% of marine organisms introduced unintentionally compared with 34% of plants and 28% of fish. Around 50% of IAS native from each region may be introduced elsewhere unintentionally.

Policy response

Figure S6 gives the cumulative number of international treaties mentioning IAS that have been written with either global or regional (more than one country) coverage for 1933 – 2015 (a total of 48 treaties), based on search results from ECOLEX (2016). Figure S6 also gives the number of countries per year that have signed one or more IAS-related international treaties in a given year for 1933–2015; 244 countries have signed one or more of the 48 treaties. Finally, Fig. S6 gives the cumulative number of global national/sub-national legislations/regulations relevant to IAS for $1980-2015$ (a total of 342 pieces of legislation/regulation; relevance score >0). The beginning of the rapid growth in the early 1990s coincides with the 1992 Convention on Biological Diversity (CBD, 1992).

Figure 5(a) shows the number of global and regional international treaties (N_{IT}) mentioning IAS for which a given country is signatory, plotted globally. France has signed the most international treaties ($N_{IT}=30$) mentioning IAS, of which 12 have global applications and 18 regional. France is followed by the UK, the Netherlands and Germany each with 24, and Spain and Italy with 23. The main differentiation between these six countries is in the number of treaties with regional scope. With its overseas territories, France is signatory to regional treaties such as the Convention on Conservation of Nature in the South Pacific (1976) and the Plant Protection Agreement for the Asia and Pacific Region (1956). As expected, Fig. 5(a) shows notable variation in N_{IT} across regions, as the majority of international treaties have a regional scope.

Out of 342 national/sub-national relevant documents put in place since 1980, 154 pieces of legislation/regulations across 70 countries have a relevance score of 3 or 4, which shows that a genuine effort is being made to manage invasive species (see Table S4). Figure 5(b) shows the maximum relevance score for those countries with one or more national/sub-national pieces of legislation/regulations. The majority of African countries, the Arabian Peninsula and Asia (India, China) have no data or only low-relevance (maximum relevance score 1 or 2) legislation/regulations. Numerous IAS legislation/regulations are focused on IAS control/management, current IAS or introductions of IAS, but not as many measures seem to be in place to prevent species from leaving countries.

DISCUSSION

The global patterns visualized reinforce the role of history, culture and trade on human-facilitated movement of species. The Global North and some newly industrialized countries (e.g. China, India, Brazil) seem to be the main recipients of IAS, along with islands that are former European colonies and which would have long histories of repeated species introductions or increased 'introduction effort' (Lockwood *et al.*, 2005) (Figs 1 & 3). The number of native species invasive elsewhere varies across countries (Fig. 2): $S_{Nat}>126$ in 36% of the 55 countries (excluding overseas territories) in the Europe region, 18% of the 61 Asia Pacific countries and 13% of the 52 Latin America plus Caribbean countries; $S_{Nat}<56$ in 55% of 58 of the African countries. Our study supports previous research highlighting economic development, with its associated international trade and globalization, as key drivers of IAS introduction (Vilà & Pujadas 2001; Meyerson & Mooney, 2007; Westphal *et al.*, 2008; Pyšek *et al.*, 2010).

Both islands and some highly developed New World countries (e.g. the USA, Australia, New Zealand) have a medium to high positive asymmetry index ($2.0 \leq K \leq 6.0$) (Fig. 3), indicating they have many more IAS in that country than species native to that country that are invasive elsewhere. This contrasts with many Western European countries with a negative to zero asymmetry index ($-2.0 \leq K \leq 0.0$). Again this reflects the implications of ongoing trade and colonial history on species invasions, as well as the singular position of islands, which is well documented (Elton, 1958; Mooney & Cleland, 2001; Courchamp *et al.*, 2003). New World countries have had a more rapid influx of IAS while the Old World has been exchanging species via trade for millennia, so the scale and 'impacts' of recent invasions are more obvious in the New World. For instance, the UK has both 'imported' and 'exported' high numbers of IAS; therefore, K is near zero. Many species that are invasive elsewhere are native to the USA, but a greater number of species have invaded the USA – resulting in positive K – partly due to the rapid influx of global populations and trade (Work *et al.*, 2005). This does not necessarily imply that New World species have a lower invasion potential than Old World species, as suggested by di Castri (1989), but rather that species immigration rates have historically been greater towards the New World (Lonsdale, 1999).

In Africa, the majority of countries (71% of 58) have a low number of recorded IAS ($S_{Inv}<27$; Fig. 1) and 88% have K ` 0 (Fig. 3), despite extensive colonization of Africa by European countries. This is probably due to limited development in these countries along with relatively limited shipping between African countries and the Global North (Wang & Wang, 2011). However, such less developed countries may have many unrecorded species and unknown impacts, as species records are closely tied to the resources available in each country to find and record species (McGeoch *et al.* 2010). Exceptions in Africa include South Africa, with a high $S_{Inv}=208$ ($S_{Nat}=100$) (Fig. 1) and Morocco and Algeria, each with a high $S_{Nat}=130$ (and, similar to the rest of Africa, a low S_{Inv}) (Figs 1 & 2). These exceptions reinforce the influence of colonization and trade on invasion patterns. Indeed, these three countries are former colonies and have major international shipping ports (World Bank, 2014). This also reflects the weight of resource availability; Pyšek *et al.* (2008) notes that two-thirds of research efforts on the African continent are accounted for by South Africa. International trade is increasing in Africa (ITC, 2012) and so the number of IAS is likely to grow, making this continent a priority for IAS research (see also Chenje & Mohamed-Katerere, 2003; Macdonald *et al.*, 2003). Similar trends are observable in the five central Asian countries, which have relatively low numbers of recorded IAS ($4<S_{Inv}<13$) (Fig. 1a, Table S3) but relatively high numbers of species native to Central Asia but invasive elsewhere ($57<S_{Nat}<100$) (Fig. 2, Table S3). With the recent oil, gas and mining development in the region, S_{Inv} is likely to increase (Dimeyeva, 2013) and countries such as Kazakhstan, Turkmenistan and Uzbekistan should also be priorities for invasion ecology research.

The dominance of plants and arthropods in the GISD (2016) and CABI ISC (2016) databases is unsurprising (Table 3). Elton (1958) observed that the spread of IAS could primarily be attributed to the movement of plants and attendant insect ‘hitchhikers’. Further analysis of the data informing Figs S2–S5 shows that 46% of recorded invasive plants may have been intentionally introduced through horticulture and the nursery trade and 21% through agriculture. This also holds for mammals, fish and other organisms that are often introduced intentionally; we found that 78% of recorded mammals and 89% of fish may have been introduced deliberately. McGeoch *et al.* (2016) found that the most recurrent pathways for IAS were escapees from horticulture and pet aquaria. These trends may also be the result of taxonomic bias in recording (e.g. Wilson *et al.*, 2007; Pyšek *et al.*, 2008). These results emphasize the role of trade in the introduction and spread of IAS, stressing not only the need for policymakers to work with industries but also, as suggested by Hulme (2015), the need to educate citizens. Further analysis of our results indicated that intentional introduction of species for environmental management such as land reclamation and erosion control accounted for 8% of introductions and also requires attention.

With 39% of recorded IAS introduced unintentionally (Fig. 4) and 22% both intentionally and unintentionally, stowaways are a major pathway of introduction largely driven by tourism (Roy *et al.*, 2014; Hulme, 2015; McGeoch *et al.*, 2016). Population flows such as migration can also represent a socio-economic driver of species introduction and spread in addition to those highlighted by Hulme (2015), which include tourism, trade and infrastructure projects. The proportion of each country’s IAS (excluding overseas territories) introduced unintentionally ranges from 25% to 100% of the total IAS recorded in that country, with 63% of countries globally having a greater proportion of species introduced unintentionally.

The continuous increase in international treaties/legislation relevant to alien species represents a growing global awareness of IAS (Figs 5 & 6) and a genuine desire from the international community to act on the matter. As might be expected, those countries with greater numbers of IAS have more targeted regulations/legislation specifically dealing with IAS, with a maximum relevance score ≥ 3 (Fig. 5b). More countries are introducing legislation to tackle IAS (García de Lomas & Vilà, 2015). Pre-emptive legislation is needed to combat IAS in those countries that currently have few legal instruments, though uptake seems good overall. This does not mean that the instruments are effective of course, and those countries at greater risk should pay careful attention to threats from IAS.

Information on legislation and regulations relevant to IAS (Fig. 5b) seems largely missing across parts of Asia, the Arabian Peninsula and the African continent. This could be the result of a lack of data for these regions or a genuine lack of policy. In the latter case, the development of legislation and regulations in those regions could (1) prevent the introduction of species or (2) help reduce the spread and impact of existing IAS, both of which are likely to be exacerbated as development continues based on the patterns and drivers observed here. Although countries are concerned about the introduction and spread of IAS within their legal boundaries, not as much attention is given by originating countries to preventing the egress of species, unless the species has known public health impacts.

To conclude, this study provides a visualization of global geographical patterns of species invasions and species origins across the majority of recorded taxa. The results support the human-mediated movement of species through time, notably with the discovery of the New World, increasing trade and globalization. Of the 1517 recorded IAS, 39% were introduced only intentionally, 26% only unintentionally and 22% both intentionally and unintentionally; 13% had no information available. Trade, including the nursery, pet and aquarium or live food trade, are the main pathway of intentional introductions. Increases in policy response towards IAS internationally and regionally show increasing efforts to act on the issue of species invasions, related particularly to exposure to IAS. The results are useful for guiding management responses and focusing research regionally, for example Africa and Central Asia can be identified as priority areas for future research efforts.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1 Global Invasive Species Database (GISD, 2016) terms used in their categories for species ‘occurrence’, ‘status’ and ‘invasiveness’ [A,B,C] and CABI Invasive Species Compendium (CABI ISC, 2016) used for their category terms in ‘absence’, ‘presence’ and ‘species’ [D,E,F]. GISD category A corresponds to CABI ISC category D and E. GISD category B and C correspond to CABI ISC category F.

Table S2 Invasive Alien Species (IAS) Relevance Scores that we attributed to ECOLEX database legislations and regulations. Scores range from 0 to 4 based on the criteria given. Legal instrument must meet one or more of the criteria to be allocated a score.

Table S3 Invasive Alien Species data. For each country (exluding overseas territories) are given S_{Inv} (# of invasive alien species (IAS) in the country) and S_{Nat}, # species native to country but alien in other countries (based on invasive native range, INR, information) with data for both based on GISD (2016) and CABI ISC (2016). Also given is each country’s IAS asymmetry index K (see Eq. (1) in main text) the # of international treaties per country (based on ECOLEX, 2016), and the number of IAS per country S_{Inv}) divided by that country’s land area (A) in km2. Bolded are the ten countries with the highest number of recorded IAS (ranked 1 to 10); these are also given in Table 2 of the main text. ISO3 code from International Organisation for Standardisation (ISO, 2014).

Table S4 National and subnational legislations and regulations relevant to Invasive Alien Species (IAS) with associated Relevance Scores, country, ECOLEX ID, title of text and document type. See Table S2 fo detailed information on the Relevance Score. Data from ECOLEX database (2016).

Figure S1 Breakdown of recorded invasive alien species by organism type. The bars are in descending order of number of species from top to bottom (see legend) with the category “other” includes the following organism types: alga, annelid, flatworm, fungus, micro-organism, mollusc, nematode, oomycete, parasites and virus. Data from CABI ISC (2016) and GISD (2016).

Figure S2 Number of invasive alien species by introduction pathways to a geographical region using chord diagrams for intentional ingress of: (a) plants, (b) arthropods, (c) fish, (d) mammals, (e) birds, and (f) reptiles. Data from CABI ISC (2016) and GISD (2016). See additional information for Figs. S2–S5 on p.3 for more detailed information on the chord diagrams and for introduction pathway abbreviations.

Figure S3. Number of invasive alien species by introduction pathways to a geographical region using chord diagrams for unintentional ingress of: (a) plants, (b) arthropods, (c) fish, (d) mammals, (e) birds, and (f) reptiles. Data from CABI ISC (2016) and GISD (2016). See additional information for Figs. S2–S5 on p.3 for more detailed information on the chord diagrams and for introduction pathway abbreviations.

Figure S4. Number of invasive alien species by introduction pathways from a geographical region using chord diagrams for intentional egress of: (a) plants, (b) arthropods, (c) fish, (d) mammals, (e) birds, and (f) reptiles. Data from CABI ISC (2016) and GISD (2016). See additional information for Figs. S2–S5 on p.3 for more detailed information on the chord diagrams and for introduction pathway abbreviations.

Figure S5. Number of invasive alien species by introduction pathways from a geographical region using chord diagrams for unintentional egress of: (a) plants, (b) arthropods, (c) fish, (d) mammals, (e) birds, and (f) reptiles. Data from CABI ISC (2016) and GISD (2016). See additional information for Figs. S2–S5 on p.3 for more detailed information on the chord diagrams and for introduction pathway abbreviations.
Figure S6. International treaties, national/sub-national legislations and regulations to do with invasive alien species as given in the ECOLEX database (2016). Shown are the following: (i) number of countries per year that have signed one or more international treaty in a given year (vertical bars) over the period 1933–2005; (ii) cumulative number of international treaties globally 1933–2015 (orange diamonds); (iii) cumulative number of relevant national/subnational legislations and regulations globally 1980–2015 (purple circles) (Relevance Score >0). Legal instruments refer to international treaties, national/subnational regulations and legislations.

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